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Hooroo mates! Phylogenomic data suggest that the closest relatives of the iconic Tasmanian cave spider *Hickmania troglodytes* are in Australia and New Zealand, not in South America

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Abstract. *Hickmania troglodytes* is an emblematic cave spider representing a monotypic cribellate spider genus. This is the only Australian lineage of Austrochilidae while the other members of the family are found in southern South America. In addition to being the largest spider in Tasmania, *Hickmania* is an oddity in Austrochilidae because this is the only lineage in the family bearing posterior book lungs, tarsal spines and an embolar process on male pedipalps. Six-gene Sanger sequences and genome scale data such as ultraconserved elements (UCEs) and transcriptomes have suggested that *Hickmania troglodytes* is not nested with the family of current classification, Austrochilidae. We studied the phylogenetic placement of *Hickmania troglodytes* using an increased taxon sample by combining publicly available UCE and UCEs recovered from transcriptomic data in a parsimony and maximum likelihood framework. Based on our phylogenetic results we formally transfer *Hickmania troglodytes* from Austrochilidae to the family Gradungulidae. The cladistic placement of *Hickmania* in the family Gradungulidae fits the geographic distribution of both gradungulids (restricted to Australia and New Zealand) and austrochilids (restricted to southern South America) more appropriately.

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Introduction

The Tasmanian Cave Spider (*Hickmania troglodytes*) (Fig. 1) is a fascinating arachnid found exclusively on the island of Tasmania and is often referred to as a 'living fossil' because this species retains the plesiomorphic configuration of two pairs of book lungs (Platnick *et al*. 2020). These nocturnal spiders build large cribellate webs than can reach up to 1.8 m in length and can be found in caves and in dark and cool cavities (Hickman 1967). The monotypic genus *Hickmania* is currently placed in the superfamily Austrochiloidea. This group of spiders forms an early diverging lineage in the evolution of araneomorph spiders (Platnick 1977; Forster *et al*. 1987; Wheeler *et al*. 2017; Fernández *et al*. 2018; Kallal *et al*. 2021; Kulkarni *et al*. 2021; Ramírez *et al*. 2021). Austrochiloids consist of two families, Austrochilidae and Gradungulidae, and are distributed in the southern hemisphere. Austrochilidae includes three genera: *Austrochilus* Gertsch & Zapfe, 1955 with seven species, *Hickmania* Gertsch, 1958 with one species and *Thaida* Karsch, 1880 with two species. All austrochilid species except *Hickmania* are distributed in Chile and Argentina. *Hickmania troglodytes* is found in Tasmania. Gradungulidae includes seven genera, all of which are distributed in either Australia or New Zealand. Four of the seven gradungulid genera are monotypic.

Lehtinen (1967) proposed a new family name (Hickmaniidae) to include *Hickmania troglodytes*. Soon after the publication of Lehtinen's groundbreaking monograph, Marples (1968) published a study about the internal anatomy of hypochiloids. In the addendum of that study, Marples mentioned that '. . .a separate superfamily Gradunguloidea is proposed to include the Hickmaniidae and the Gradungulidae' (p. 31), suggesting close affinities between *Hickmania* and Gradungulidae. However, Forster *et al*. (1987) rejected this family name and placed *Hickmania* within the family Austrochilidae in a unique subfamily, Hickmaniinae. Austrochilidae thus includes two subfamilies: Austrochilinae, with *Austrochilus* and *Thaida* (from southern South America), and Hickmaniinae, that includes the monotypic *Hickmania* (from Tasmania). All Austrochilinae have one pair of book lungs and a posterior tracheal respiratory system and Hickmaninae have two pairs of book lungs (Zapfe 1955; Platnick 1977; Forster *et al*. 1987; Ramírez *et al*. 2021). Murphy and Roberts (2015) proposed a synonymy of *Hickmania* with *Thaida*, however, a detailed justification for this proposal was not provided.

Fig. 1. Male, from Saint Columba Falls (*A*) and female, from Weldborough Pass (*B*) of *Hickmania troglodytes*, from Tasmania. The characteristic sinuous second metatarsi of the male are used to grasp the female chelicerae during mating (photos by G. Hormiga).

The morphology-based phylogenetic analysis of Griswold *et al*. (2005, fig. 216–219) included three austrochiloid genera, recovering *Hickmania* as sister to *Gradungula* Forster, 1955 (Gradungulidae), with this latter clade being the sister group of *Thaida* (Austrochilidae). In the six-marker Sanger sequencing-based phylogeny of Araneae, Wheeler *et al*. (2017) recovered *Hickmania* as a sister group to Archoleptonetidae and this whole clade formed a sister group to Gradungulidae, however, these relationships received low bootstrap support. Various genomic scale datasets such as transcriptomes analysed as amino acids (Fernández *et al*. 2018, Kallal *et al*. 2021), and as nucleotides and ultra-conserved elements (UCEs, Kulkarni *et al*. 2021; Ledford *et al*. 2021; Ramírez *et al*. 2021) recovered *Hickmania* as a sister group to Gradungulidae with strong bootstrap support.

In this study, we reassessed the cladistic placement of *Hickmania* using a combination of UCE and transcriptome sequence data. Based on our phylogenetic results we place the genus *Hickmania* in the family Gradungulidae.

Materials and methods

Taxon sampling

The ultraconserved sequences (UCEs) for this study were obtained from publicly available transcriptomes and UCEs (we sequenced some of these) that were targeted using Arachnida and the 'spider-specific' Spider2Kv1 probe sets (Starrett *et al*. 2017; Kulkarni *et al*. 2020). Because the aim of this study is to assess the placement of *Hickmania troglodytes*, we sampled lineages from the families Austrochilidae, Gradungulidae, Leptonetidae and Archoleptonetidae. Two taxa of Palpimanidae (*Palpimanus gibbulus* Dufour, 1820 and *Otiothops birabeni* Mello-Leitão,

1945) were used to root the phylogeny. See Table 1 for list of taxa, sequence details and the locus coverage.

Transcriptome Assembly and UCE recovery

We ran the perl script for Rcorrector (ver. 2, see https://github.com/mourisl/rcorrector; Song and Florea 2015) for error correction and downstream efficiency before assembly. The low-quality reads and adapters were trimmed using Trim Galore! (ver. 0.2.6, see http://www.bioinformatics.babraham.ac.uk/projects/trim_galore, accessed 5 June 2021) by setting the quality parameter to 30 and a phred cut-off to 33; reads shorter than 25 bp were discarded. Ribosomal RNA was filtered using the default settings in Bowtie (ver. 2.9.9, see https://github.com/BenLangmead/bowtie; Langmead and Salzberg 2012). *De novo* strand-specific assemblies were generated using Trinity (ver. 2.0.6, see https://github.com/trinityrnaseq/trinityrnaseq; Grabherr *et al*. 2011; Haas *et al*. 2013) with a path reinforcement set to 75. Redundancy reduction was done using CD-HIT-EST (see http://weizhong-lab.ucsd.edu/cd-hit/; Fu *et al*. 2012) with 95% global similarity.

The FASTA files of transcriptomes resulting from CD-HIT-EST were converted to 2-bit format using faToTwoBit (see http://hgdownload.soe.ucsc.edu/admin/exe/linux.x86_64/; Kent 2002). Subsequently, in the PHYLUCE environment (see https://phyluce.readthedocs.io/en/latest/tutorial-three.html), we created a temporary relational database to summarise probe to assembly match using: phyluce_probe_run_multiple_lastzs_sqlite function on the 2-bit files. The ultraconserved loci were recovered by the phyluce_probe_slice_sequence_from_genomes command. The resulting FASTA files were treated as contigs and used to match the reads to the Spider2Kv1 probes.

GC content

GC content can influence the phylogenetic relationships reconstructed using genome scale data (Benjamini and Speed 2012). To address this, we computed GC content in each taxon in the concatenated alignment using BBMap (see https://github.com/BioInfoTools/BBMap).

Phylogenomic analyses

The assembly, alignment, trimming and concatenation of data were done using the PHYLUCE pipeline. We applied gene occupancies of 1, 10, 25 and 40%. We screened for orthologous and duplicate loci with the minimum identity and coverage of 65 and 65 matches. Phylogenetic analyses were performed on the unpartitioned nucleotide data using IQ-TREE (ver. 1.7-β, http://www.iqtree.org/; Nguyen *et al*. 2015). Model selection was allowed for each dataset using the TEST function (see http://www.iqtree.org/; Hoang *et al*. 2018; Kalyaanamoorthy *et al*. 2017). Nodal support was estimated by 1000 UFBoot replicates (Hoang *et al*. 2018) and Shimodaira–Hasegawa-like approximate likelihood ratio test (SH-aLRT) (Guindon *et al*. 2010). To reduce the risk of overestimating branch support with UFBoot due to model violations, we appended the command -bnni. Using this command, the UFBoot optimises each bootstrap tree using a hill-climbing nearest neighbour interchange (NNI) search based on the corresponding bootstrap alignment (Hoang *et al*. 2018).

Furthermore, we analysed unpartitioned concatenation of loci as nucleotides using parsimony and the model-based maximum likelihood. Parsimony analyses were performed using TNT (ver. 1.5, see http://www.lillo.org.ar/phylogeny/tnt/; Goloboff *et al*. 2008) Linux version using gaps treated as missing data and following settings were used for reconstructing the cladogram: *xmul: replications 4 hits 4 ratchet 20 drift 20 fuse 20 rss xss css.xmu;bb;le;ne**; Nodal supports were estimated using 1000 bootstrap replicates and the Group present or Contradicted frequency metric of Goloboff *et al*. (2003). This latter measure indicates the difference in frequency between a group and the most frequent contradictory group.

Table 1. List of taxa included in this study with accession numbers for NCBI Sequence Read Archive and locus count obtained using Spider2Kv1 probes at 65% minimum identity and coverage values

Family	Taxon	Loci	Accession code
Archoleptonetidae	*Archoleptoneta gertschi*	288	SRR11292747
Archoleptonetidae	*Archoleptoneta schusteri*	350	SRR6997753
Archoleptonetidae	*Darkoneta* sp. JL Lep6A1	467	SRR11292762
Austrochilidae	*Austrochilus forsteri*	494	SRR6997749
Austrochilidae	*Thaida peculiaris*	46	SRR11292744
Gradungulidae	*Gradungula* sp. GH2710	1081	SRR10291863
Gradungulidae	*Hickmania troglodytes*	438	SRR6997862
Gradungulidae	*Hickmania troglodytes* HW_0197	93	SRR7363164
Gradungulidae	*Pianoa isolata*	320	SRR6998914
Gradungulidae	*Progradungula otwayensis*	395	SRR6998916
Gradungulidae	*Spelungula cavernicola*	70	SRR11292788
Gradungulidae	*Tarlina* sp.	480	SRR6998918
Gradungulidae	*Tarlina woodwardi*	27	SRR11292783
Leptonetidae	*Appaleptoneta barrowsi*	33	SRR11292770
Leptonetidae	*Barusia insulana*	16	SRR11292742
Leptonetidae	*Calileptoneta californica*	897	SRR3144085
Leptonetidae	*Cataleptoneta edentula*	27	SRR11292778
Leptonetidae	*Cataleptoneta semipinnata*	23	SRR11292775
Leptonetidae	*Chisoneta chisosea*	47	SRR11292769
Leptonetidae	*Leptoneta convexa*	42	SRR11292764
Leptonetidae	*Jingneta foliiformis*	675	SRR6425914
Leptonetidae	*Leptoneta infuscata*	45	SRR11292765
Leptonetidae	*Leptonetela thracia*	52	SRR11292741
Leptonetidae	*Neoleptoneta capilla*	33	SRR11292763
Leptonetidae	*Ozarkia alabama*	66	SRR11292761
Leptonetidae	*Sulcia cretica violacea*	61	SRR11292776
Leptonetidae	*Tayshaneta microps*	31	SRR11292771
Palpimanidae	*Otiothops birabeni*	386	SRR6998652
Palpimanidae	*Palpimanus gibbulus*	527	SRR6998653

Results and discussion

Our complete dataset (1% occupancy) included a total of 1246 loci, 527 519 sites and 52 434 parsimony informative sites. The 10% occupancy also recovered 1246 loci whereas the 25% occupancy dataset recovered 274 UCE loci. All datasets analysed with parsimony and maximum likelihood frameworks recovered Archoleptonetidae as a sister group to a clade including Austrochiloidea as a sister group to Leptonetidae. Within the austrochilioid clade,

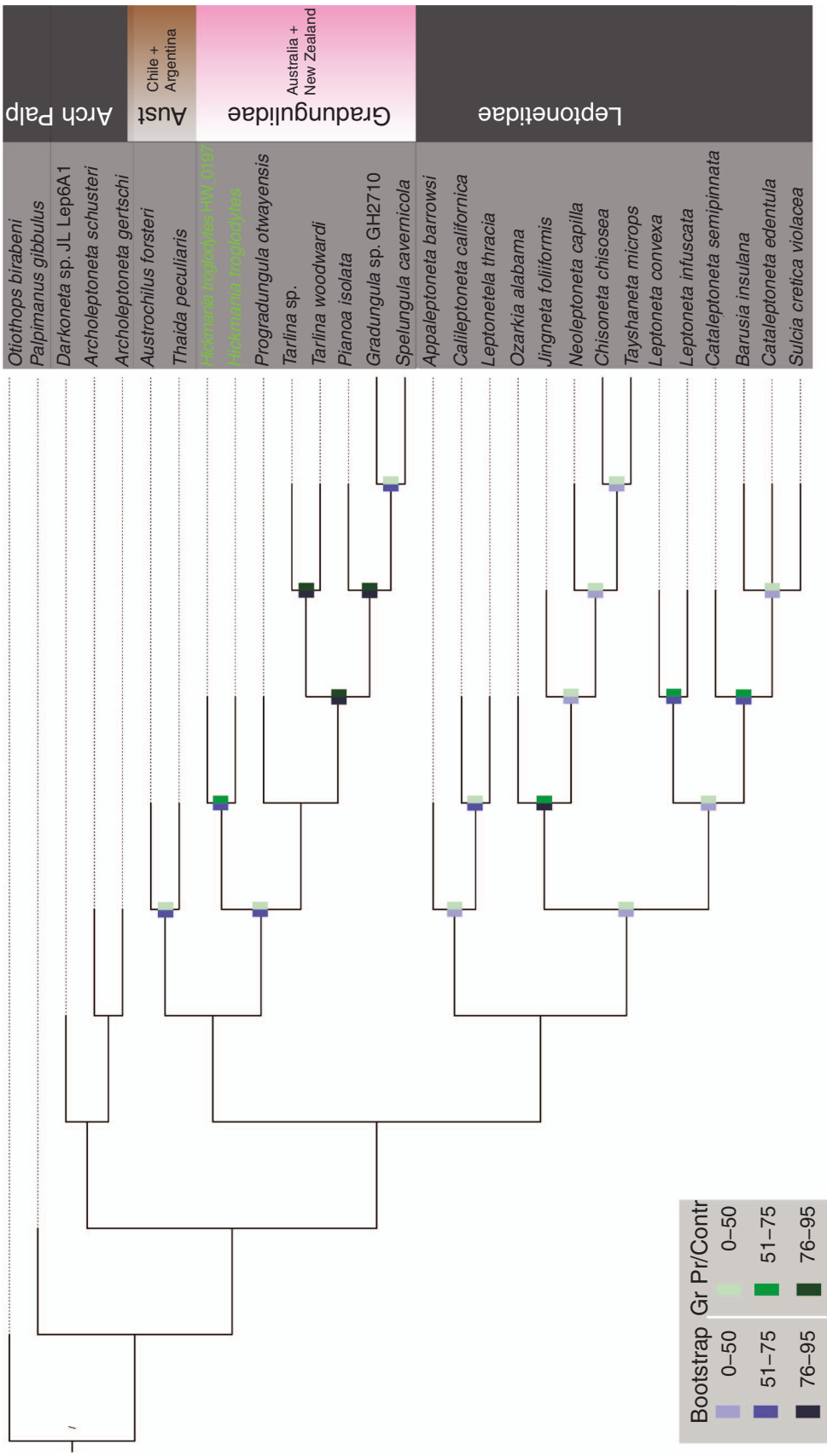

Fig. 2. Parsimony cladogram reconstructed using TNT for the unpartitioned 25% occupancy dataset. Support measures of bootstrap and Group Present or Contradicted (Gr Pr/Contr) of Goloboff *et al.* (2003) are indicated at the nodes.

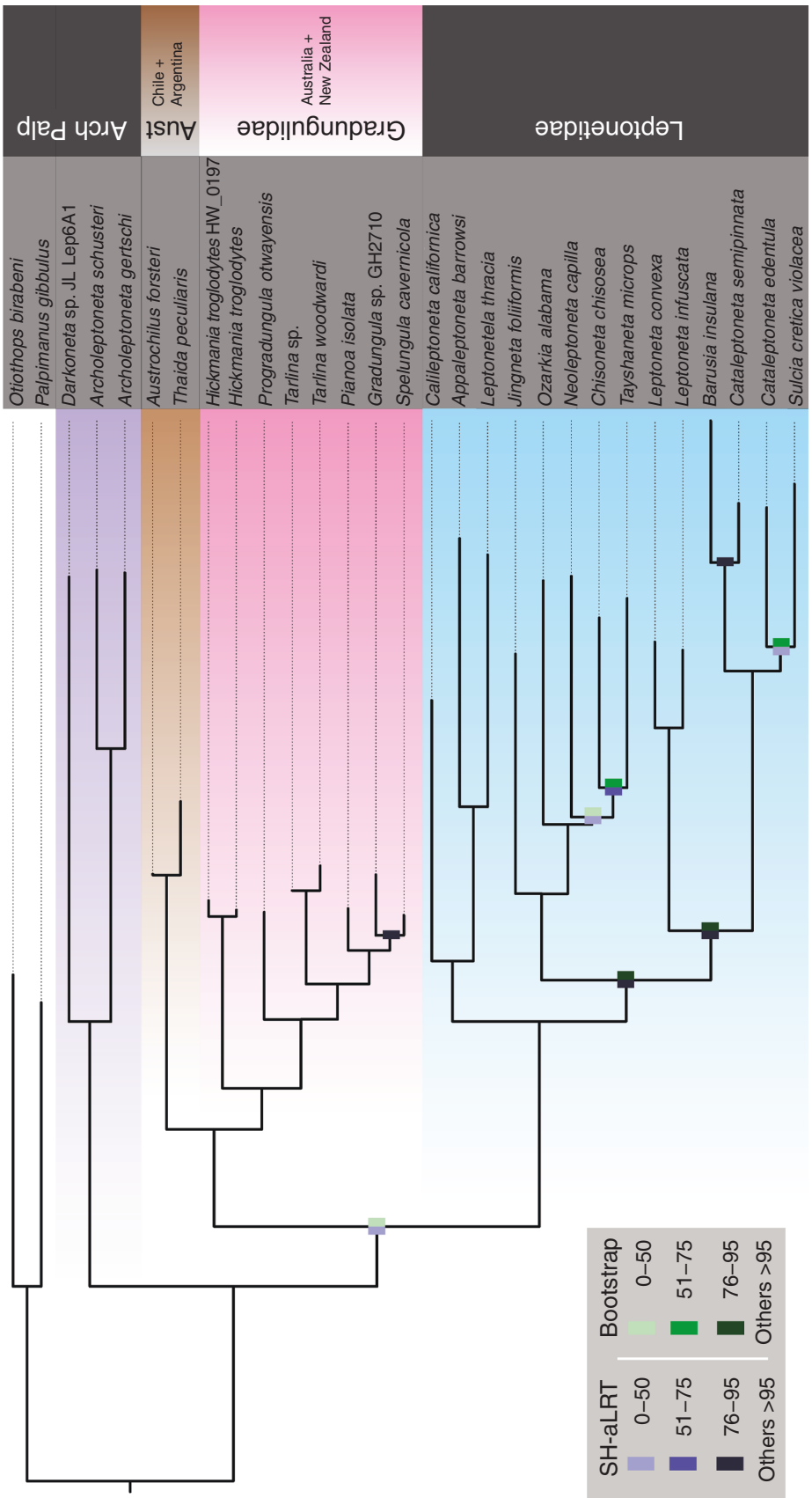

Fig. 3. A maximum likelihood phylogeny reconstructed using IQ-TREE for 25% occupancy dataset. Support measures of bootstrap and Shimodaira–Hasegawa approximate likelihood ratio test are indicated at the nodes.

Gradungulidae was the sister group of *Hickmania troglodytes*, which together formed a sister group to Austrochilidae (Fig. 1, 2, and Fig. S1–S2 of the Supplementary material). Differences observed within the leptonetid relationships were as follows: the 1 and 10% datasets recovered a clade containing *Leptoneta* group plus *Paraleptoneta* group as a sister group to a clade including *Calileptoneta* group plus *Protoleptoneta* group. In 25% occupancy phylogeny, the *Calileptoneta* group was the sister group of all other leptonetids. Both alternative relationships were strongly supported (100% UFBoot). GC content was higher in *Ozarkia alabama* (Gertsch, 1974) and *Archoleptoneta gertschi* Ledford & Griswold, 2010 as compared to other branches of the tree (Fig. S3–S4 of the Supplementary material). We reanalysed our dataset after pruning these two taxa but this did not affect the placement of *Hickmania troglodytes* (Fig. S5–S6 of the Supplementary material).

A new family placement for Hickmania troglodytes

Our phylogenetic results recovered *Hickmania* as the sister group of Gradungulidae (Fig. 2, 3). As aforementioned, this phylogenetic placement has been previously obtained with UCEs and transcriptomes analysed, and nucleotides and amino acids (Fernández *et al*. 2018, Kallal *et al*. 2021, Kulkarni *et al*. 2021; Ledford *et al*. 2021; Ramírez *et al*. 2021). The current inclusion of *Hickmania* in the family Austrochilidae renders austrochilids a paraphyletic group. Also, *Thaida* and *Hickmania* do not form a clade (Fig. 2, 3) and thus this does not support the synonymy of these genera proposed by Murphy and Roberts (2015).

Interestingly, we find some shared morphological traits between gradungulids and *Hickmania*, such as the presence of tarsal spines, retention of the posterior book lungs (in contrast with the tracheae of the austrochilid genera *Austrochilus* and *Thaida*; Zapfe 1955; Ramírez *et al*. 2021) and presence of a process in the embolus (Forster *et al*. 1987, fig. 343–345; such embolic process is absent in *Austrochilus* and *Thaida*) that is also present in gradungulids (Michalik *et al*. 2013, fig. 5A–C). Furthermore, the members of family Austrochilidae are distributed in Chile and Argentina and the only member from Australia is *Hickmania troglodytes*. On the other hand, Gradungulidae is known from Australia and New Zealand. Thus, the cladistic placement of *Hickmania* in the family Gradungulidae fits the geographic distribution of both gradungulids (restricted to Australia and New Zealand) and austrochilids (restricted to southern South America) more appropriately. The biogeographic analysis of Ledford *et al*. (2021, fig. 6) suggests the crown age of the Austrochiloidea clade to be *c.* 115 Ma. These authors hypothesise that a vicariance event explains the divergence of the Gradungulidae and Austrochilidae lineages.

In summary, the morphological features and geographic distribution of austrochilids and gradungulids fit better on the new phylogenetic hypothesis derived from the phylogenomic data. We propose the placement of the genus *Hickmania* within Gradungulidae to fulfill the classification requirement of taxon monophyly. The expression used in the title of this paper ('Hooroo mates!') is taken from an Australian slang word for 'goodbye.'

Classification

Araneae Clerck, 1758
Opisthothele Pocock, 1892
Araneomorphae Smith, 1902
Superfamily Austrochiloidea Zapfe, 1955
Family Austrochilidae Zapfe, 1955

Type genus: *Austrochilus* Gertsch and Zapfe, in Zapfe (1955).

Composition

Austrochilus Gertsch and Zapfe, in Zapfe (1955); *Thaida* Karsch, 1880.

Distribution

Chile, Argentina.

Family Gradungulidae Forster, 1955

Type genus: *Gradungula* Forster, 1955.

Composition

Gradungula Forster, 1955; *Kaiya* Gray, 1987; *Hickmania* Gertsch, 1958 **new family placement**; *Macrogradungula* Gray, 1987; *Pianoa* Forster, 1987; *Progradungula* Forster & Gray, 1979; *Spelungula* Forster, 1987; *Tarlina* Gray, 1987.

Gradungulids are classified into two subfamilies, Hickmaniinae Lehtinen 1967, and Gradungulinae Forster, 1955; the latter includes the remaining six gradungulid genera. Diagnoses and generic descriptions of gradungulids, including *Hickmania*, are provided in Forster *et al*. (1987).

Conflicts of interest

The authors declare that they have no conflicts of interest.

Declaration of funding

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Supplementary material

Hooroo mates! Phylogenomic data suggest that the closest relatives of the iconic Tasmanian cave spider *Hickmania troglodytes* are in Australia and New Zealand, not in South America

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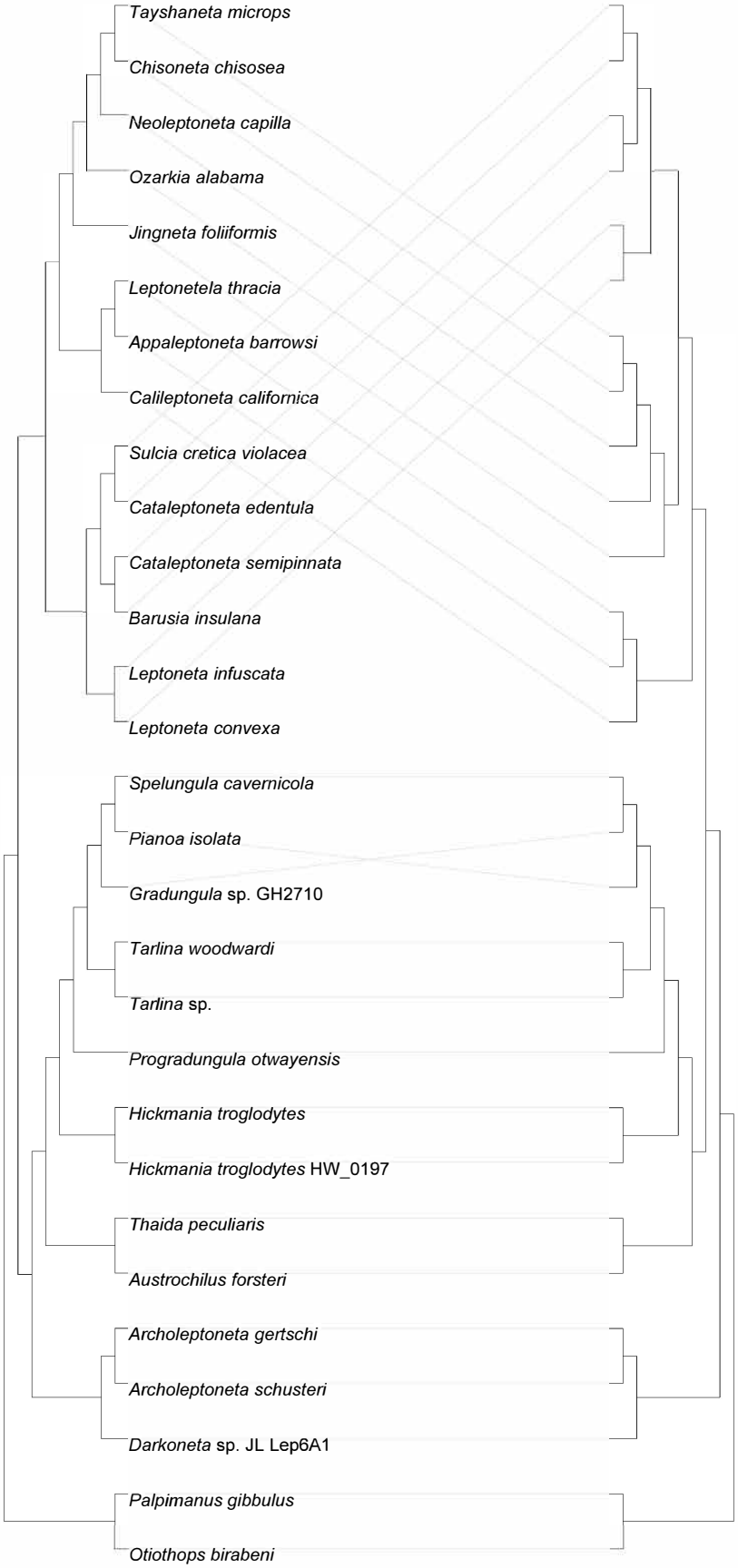

Fig. S1. Comparison of maximum likelihood trees constructed using unpartitioned data for occupancies 1% (same as 10%) [left] to 25% datasets.

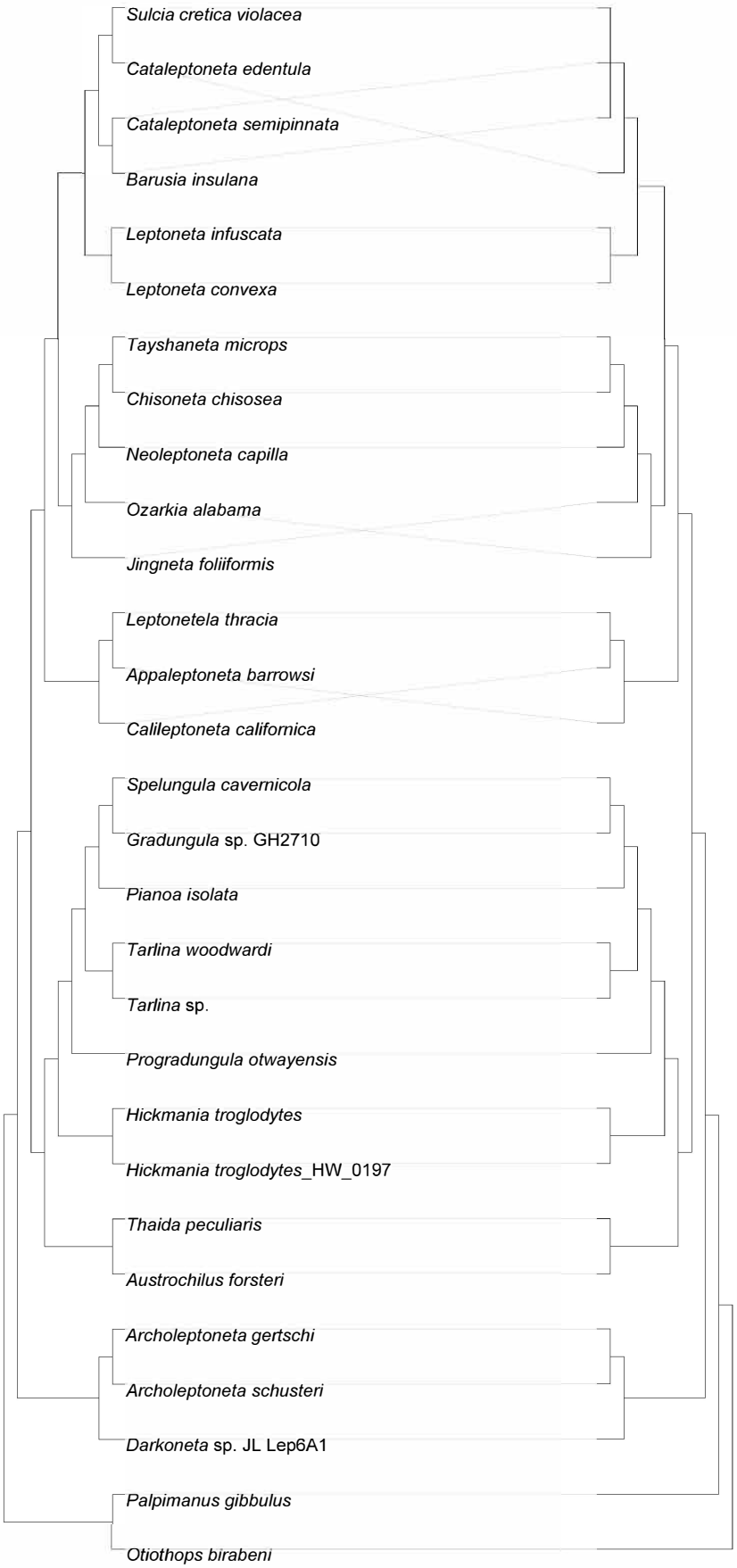

Fig. S2. Comparison of maximum likelihood [left] and parsimony [right] constructed using unpartitioned data for 25% occupancy dataset.

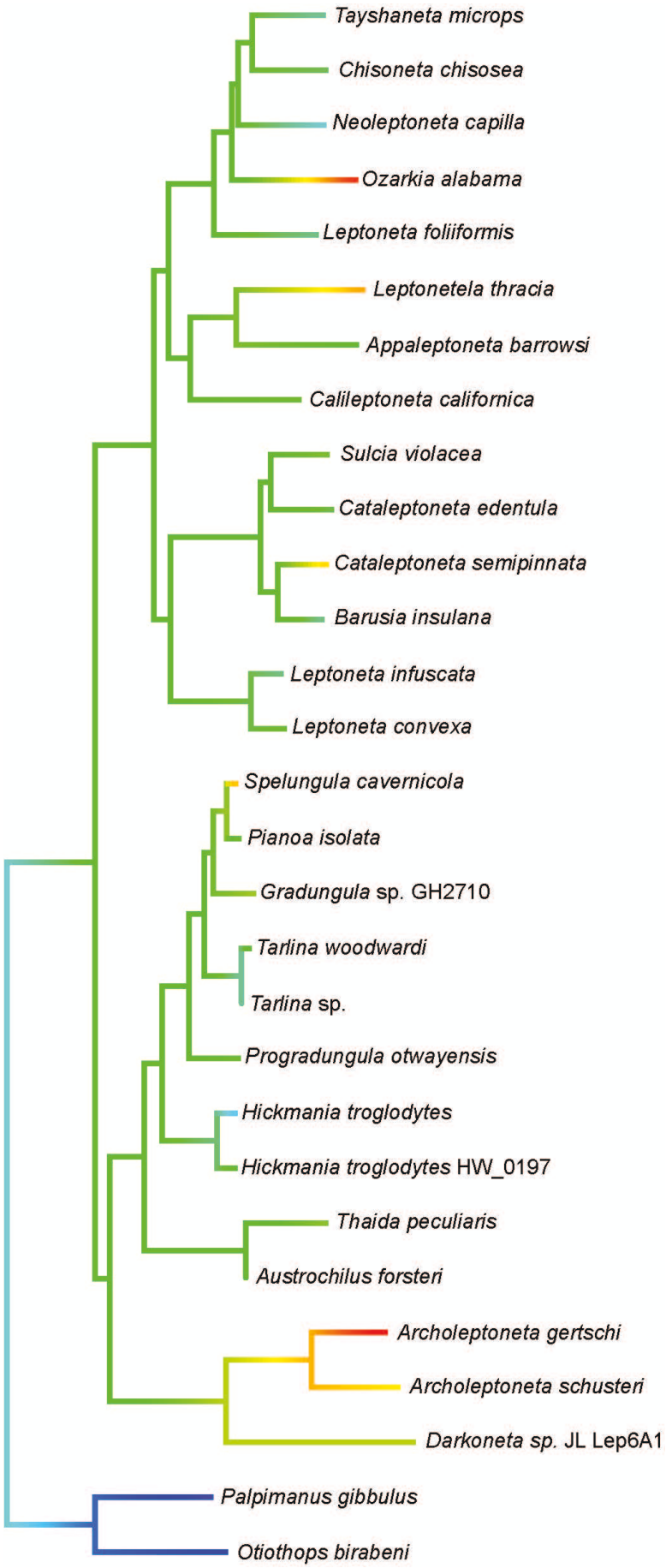

Fig. S3. GC content in the 10% occupancy datasets maps of their phylogenetic trees in the respective figures.

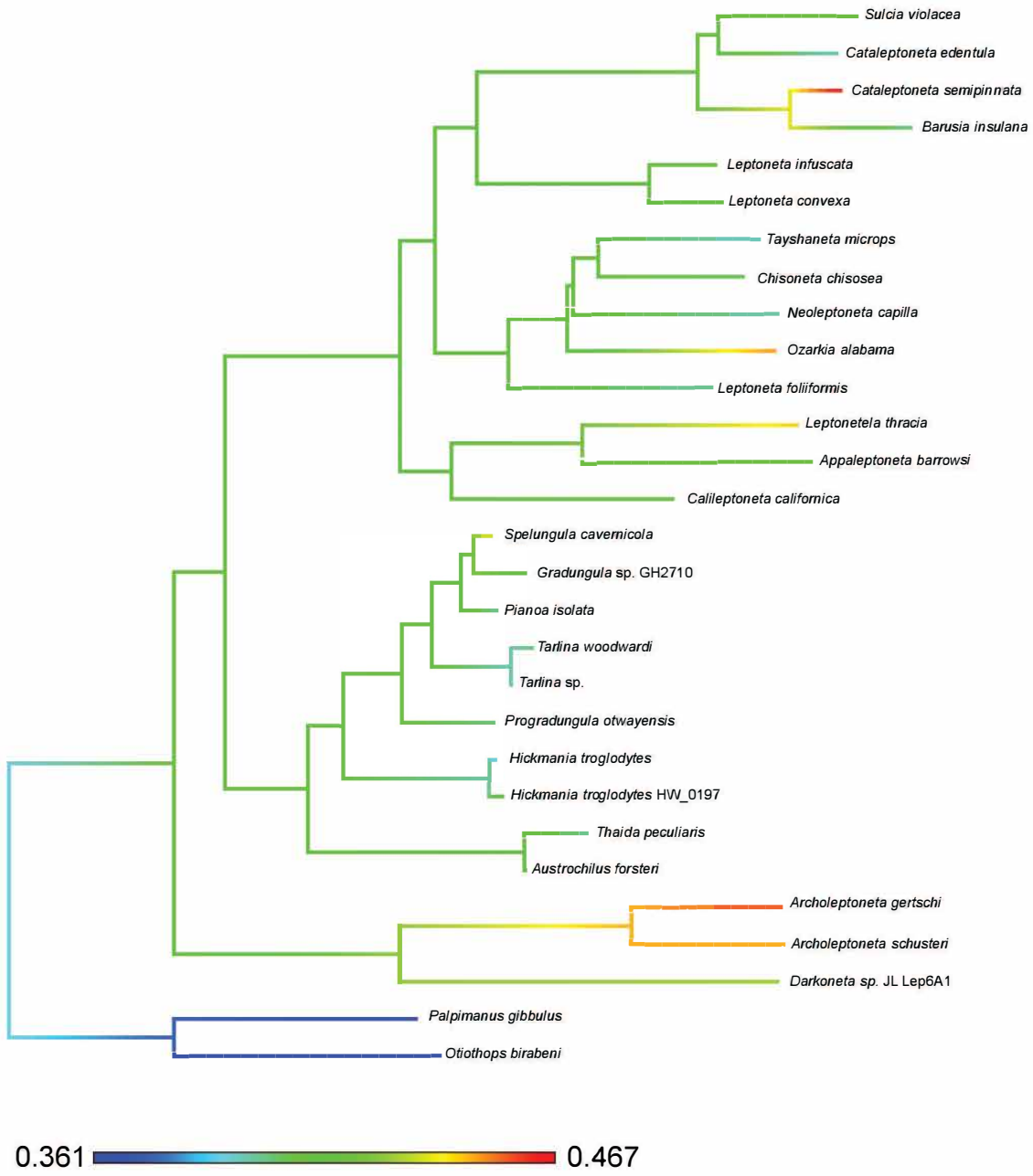

Fig. S4. GC content in the 25% occupancy datasets maps of their phylogenetic trees in the respective figures.

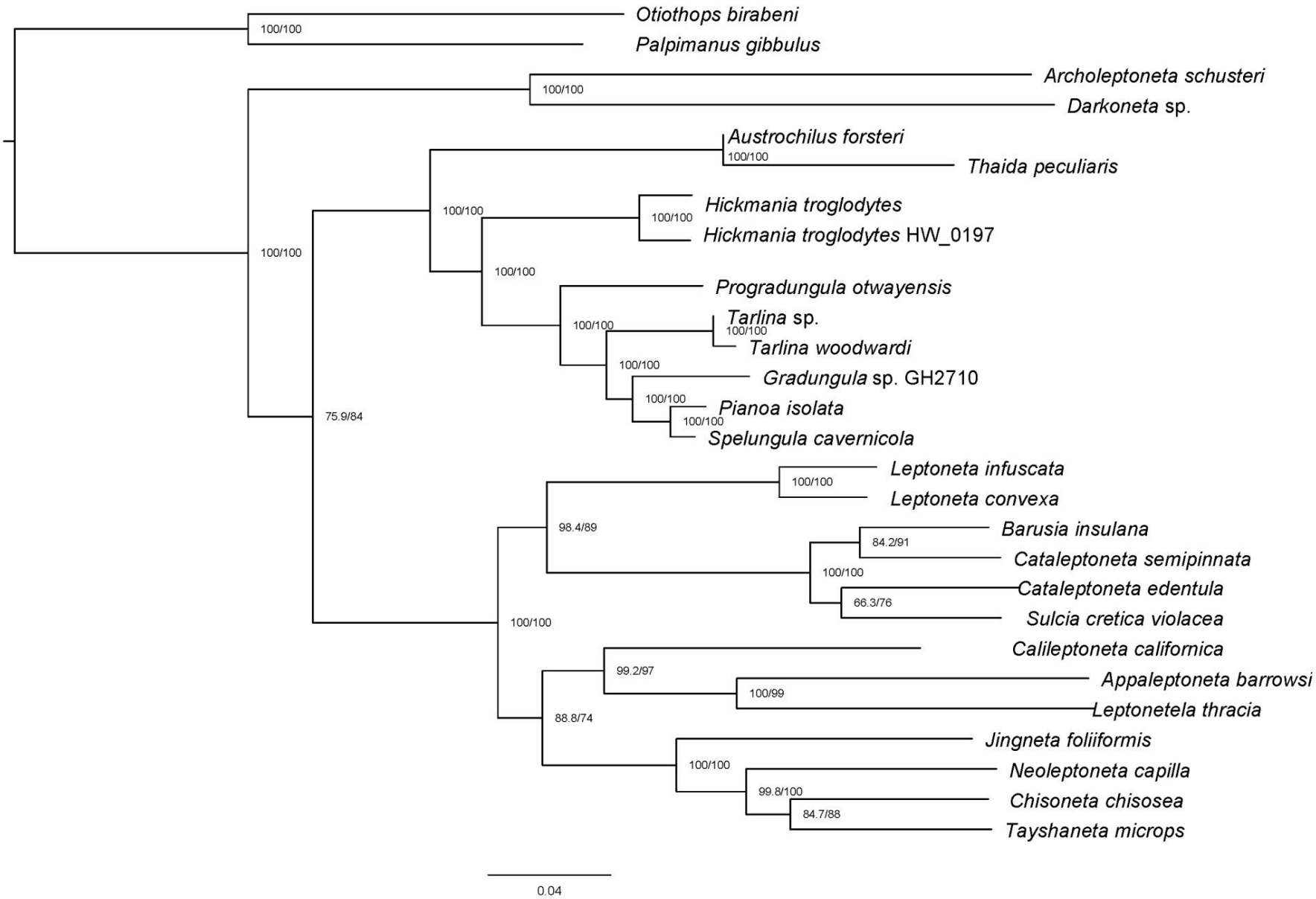

Fig. S5. Maximum likelihood trees in the 10% (same locus count as 1%) respectively with two taxa (*Archoleptoneta gertschi* and *Ozarkia*) with high GC-content were pruned.

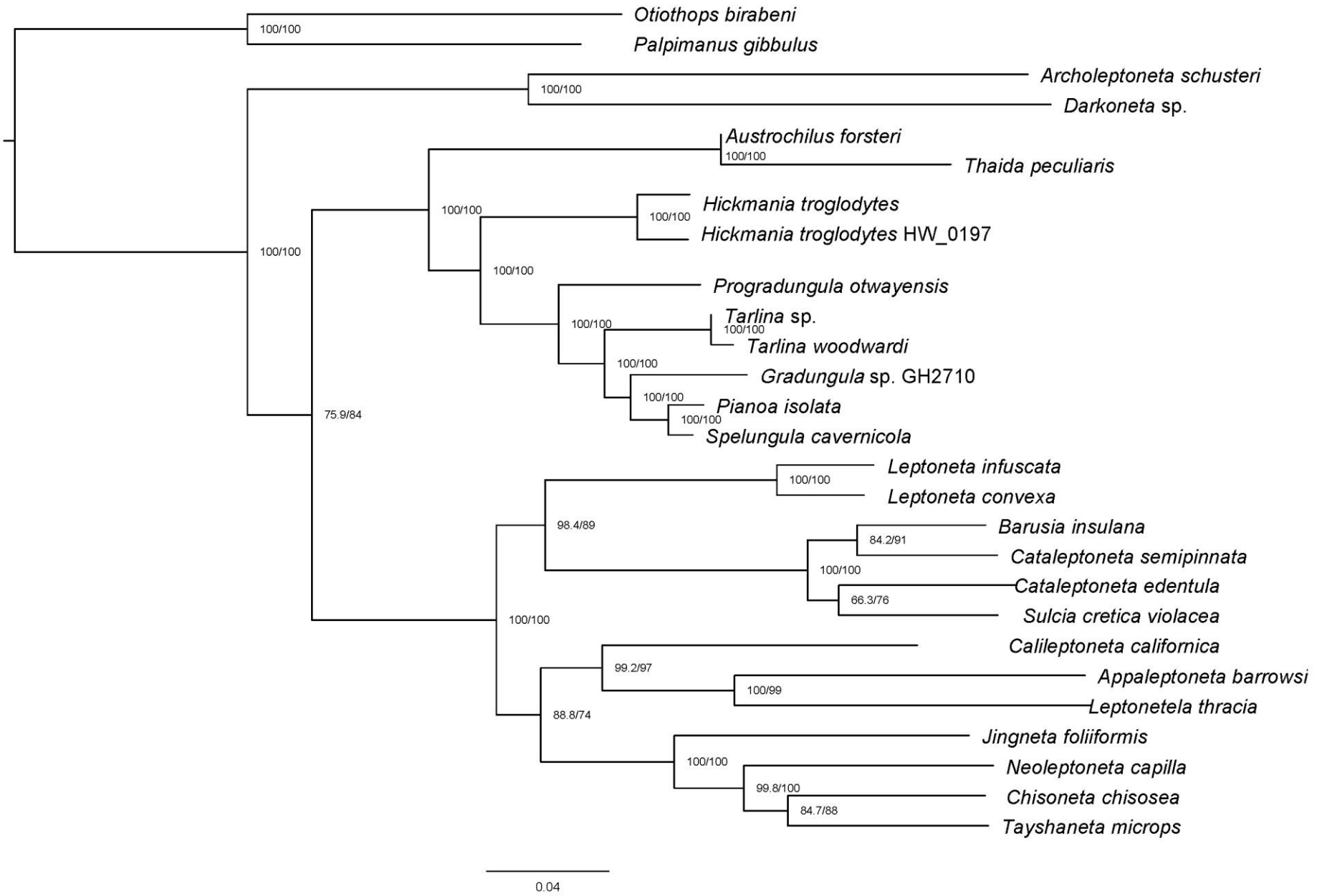

Fig. S6. Maximum likelihood trees in the 25% occupancies respectively with two taxa (*Archoleptoneta gertschi* and *Ozarkia*) with high GC-content were pruned.